

THE IDENTITY OF *TRENTEPOHLIA* ALGAE (CHLOROPHYTA: TRENTEPOHLIALES)
FROM POINT LOBOS STATE RESERVE AND THE SAN FRANCISCO REGION,
CALIFORNIA

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ABSTRACT

Terrestrial chlorophyte algae of the order Trentepohliales are found in humid habitats around the world. Although most diverse and abundant in the tropics, on a global scale the group is nearly cosmopolitan. The most distinctive macroscopic trait of the Trentepohliales is their orange, golden, or red color, which is due to the accumulation of carotenoid pigments. Orange algae of the genus *Trentepohlia*, the most species-rich genus in the order, can be found growing on trees, rocks, and other substrates along the Pacific Coast of the United States, including the San Francisco Bay region. Perhaps the best known site for these algae is at Point Lobos State Reserve in Carmel, CA. The orange algae at this site are often referred to by California naturalists as “*Trentepohlia aurea*” or “*Trentepohlia aurea* var. *polycarpa*”. Given the challenges in identifying species in this genus and some confusion about nomenclature, we sampled *Trentepohlia* at Point Lobos and elsewhere in the region to clarify the identity of these algae. We confirm that the *Trentepohlia* at Point Lobos (and most of the *Trentepohlia* we sampled at other sites) are *T. flava*, which was long considered to be a form of *T. aurea* and was often reported under the heterotypic synonym *T. aurea* var. *polycarpa*. *Trentepohlia abietina* was the only other species recorded and our observations suggest the possibility that in this region the two species may exhibit different substrate preferences (*T. flava* generalist on many different substrates, *T. abietina* limited to tree bark).

Key Words: *Trentepohlia*, *Trentepohlia abietina*, *Trentepohlia abietina* var. *corrugata*, *Trentepohlia aurea*, *Trentepohlia aurea* var. *polycarpa*, *Trentepohlia flava*, *Trentepohliales*.

The order Trentepohliales is a group of terrestrial green algae widespread in habitats characterized by high atmospheric humidity (Printz 1939; Chapman 1984). These algae are most diverse and abundant in humid tropical regions, where the majority of the species occur. On a global scale, however, their distribution is nearly cosmopolitan. In recent decades, these algae have drawn the attention of specialists due to several intriguing ultrastructural features (Chapman and Henk 1986; López-Bautista et al. 2002) and their peculiar evolutionary status as a highly diverse terrestrial group in a class (Ulvophyceae) composed mainly of marine benthic algae (López-Bautista and Chapman 2003). Members of this group, however, were already known to early naturalists of the 18th century, who provided the first species descriptions (e.g., Linnaeus 1753; Wiggers 1780). The most distinctive macroscopic trait of the Trentepohliales is their orange, golden, or red color, which is due to the accumulation of carotenoid pigments (particularly β -carotene). Members of this group can be recognized as brightly colored patches

or tufts growing on the surface of many aerial substrates, such as rocks, tree bark, leaves, twigs, fruits, soil, woodwork, and concrete. They are usually most conspicuous when growing in sun-exposed habitats, where the high irradiance stimulates the production of carotenoids.

At present, the order Trentepohliales includes approximately 115 species (Guiry and Guiry 2017), classified in the genera *Cephaleuros* Kunze, *Phycopeltis* Millardet, *Printzina* Thompson & Wujek, *Stomatochroon* Palm, and *Trentepohlia* Martius. The presence of Trentepohliales in the United States has been long known, particularly in the warm and humid southeastern states, where species of the genus *Cephaleuros* grow epiphytically or endophytically on or in the leaves of many vascular plants (Brooks et al. 2015). However, Trentepohliales are not restricted to these regions, and populations of these algae also commonly occur in many humid maritime areas of the Pacific Coast. In this case, the genus involved is *Trentepohlia*, the earliest-known and most species-rich genus in the order. *Trentepohlia* algae are



FIG. 1. Appearance of *Trentepohlia* in field populations sampled along the California coast. Top left: *T. flava* on rock (Point Lobos State Reserve). Top right: *T. flava* on cypress (Land's End). Middle left: *T. flava* on rock (Point Lobos State Reserve). Middle right: *T. flava* on dead cypress (Point Lobos State Reserve). Bottom left: *T. abietina* on tree (Presidio). Bottom right: *T. abietina* var. *corrugata* and *T. flava* on cypress tree (Great Highway). Photos by James Sikes.

composed of uniseriate filaments variously branched and joined to form dense tufts or thin crusts. Species of this genus reproduce sexually with the production of biflagellate gametes in globular or egg-shaped gametangia; asexual reproduction involves quadri-flagellate zoospores produced in globular or egg-shaped sporangia borne at the top of a cell with a characteristic retrorsely bent neck (suffultory cell). The main taxonomic characters used for morphological identification of *Trentepohlia* species are shape and size of cells, branching pattern, presence/absence of hair-like cells, and position and habit of gametangia and zoosporangia. However, it is known that some of these features may vary under different environmental conditions, making species delimitation sometimes uncertain. For this reason *Trentepohlia* is considered a taxonomically complex genus, in which morphological identification can be difficult (Rindi and Guiry 2002).

Many naturalists in California are familiar with a conspicuous orange-colored green alga seen growing on aerial substrates, particularly the bark of trees (most famously on Monterey cypress, *Hesperocyparis macrocarpa* [Hartw.] Bartel). Such growths are common in the whole coastal area of northern and central California, but are particularly well developed at certain sites, such as Point Lobos State

Reserve (Fig. 1). These algae are sometimes referred to as *Trentepohlia aurea* var. *polycarpa*, presumably referring to *Trentepohlia aurea* var. *polycarpa* (Nees and Montagne) Hariot, but most sources refer to them simply as *Trentepohlia aurea*, implying *Trentepohlia aurea* (Linnaeus) Martius. We became curious about the validity of these identifications and made field collections with the goal of clarifying the identity of this widespread alga.

METHODS

We obtained 39 samples of *Trentepohlia* from seven different sites in the San Francisco region (Table 1). Most samples were collected from Monterey cypress bark, where the most obvious growths were observed, but they were also found on other substrates (Table 1). The samples were allowed to air dry indoors before being placed in Ziploc bags and mailed to Università Politecnica delle Marche, where they were processed by Fabio Rindi (Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Italy). The samples were examined by light microscopy and identified based on morphological features, using the main taxonomic treatments for the genus *Trentepohlia* (Hariot 1889; Printz 1939; Cribb 1970; Sarma 1986). Voucher



FIG. 2. Morphology of *Trentepohlia flava*. A. habit of erect axes; scale bar: 100 μ m. B. habit of an erect axis with cells of various shapes and sizes; scale bar: 150 μ m. C. habit of erect axes bearing some empty gametangia; scale bar: 100 μ m. D. apex of erect axis showing apical cell with pectic cap; scale bar: 30 μ m. E. habit of erect axes bearing empty gametangia; scale bar: 100 μ m. F. detail of a gametangium borne on a short lateral branch, with heavily corrugated surface; scale bar: 30 μ m. Photos by Fabio Rindi.

specimens are conserved in the personal herbarium of Fabio Rindi.

RESULTS

Microscopic observation revealed that the samples belonged to two different species: *Trentepohlia flava* (Kützinger) De Toni and *T. abietina* (Flotow) Hansgirg. The distinction between these species was unambiguous and no uncertainties in their identifications were found. The two species were readily distinguished based on the size of the erect axes, width of the cells, and corrugation of the cell walls.

Trentepohlia flava was the dominant species, being recorded in 36 of the 39 samples; in 35 samples it was the only species present, whereas in one sample it was mixed with *T. abietina* var. *corrugata* (Leighton) Cribb. All samples from Point Lobos State Reserve included only *T. flava*. *Trentepohlia flava* occurred on tree bark, but also on wooden fences and rocks. Specimens of *T. flava* consisted of erect axes up to 1.5 mm tall, unbranched to sparsely branched with irregular or unilateral pattern, arising from a limited base of prostrate axes (Fig. 2A, B, C). Cells were cylindrical or slightly swollen, 15–20 (up to 25) μ m wide and 1.5–6 times as long as wide, with a thick and heavily corrugated cell wall. A well-developed

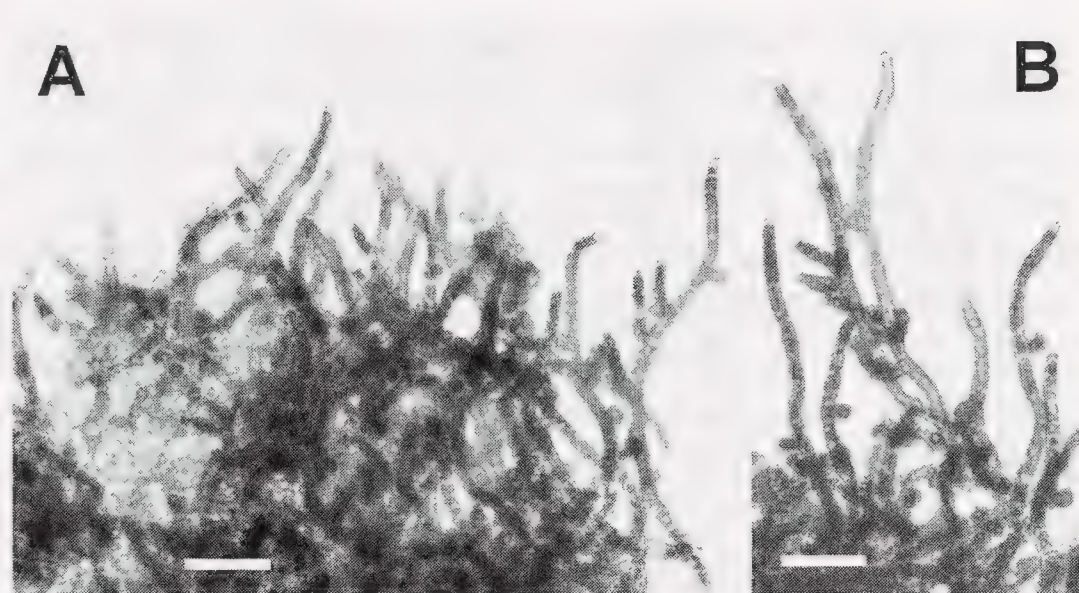


FIG. 3. Morphology of *Trentepohlia abietina*. A. habit; scale bar: 50 μ m. B. detail of some erect axes; scale bar: 50 μ m. Photos by Fabio Rindi.

pectic cap occurred at the top of each apical cell (Fig. 2D). Gametangia were present in the majority of the samples of *T. flava*; these were subglobular to egg-shaped, 25–36 (up to 40) μ m wide, lateral or apical on the erect axes or apical at the top of short lateral branches (Fig. 2C, E, F). Their surface was also heavily corrugated (Fig. 2F). Release of gametes was not observed.

Trentepohlia abietina was found in four samples. Three of these (Presidio 1, 2, and 3), all growing on tree bark, were identified as the nominate form of *T. abietina*, whereas a fourth, identified as *T. abietina* var. *corrugata*, was collected from the bark of a cypress tree beside the Great Highway (Table 1). *Trentepohlia abietina* formed thin turfs consisting of numerous interwoven specimens (Fig. 3A); each specimen consisted of one or more erect axes, unbranched or irregularly branched, up to 500 μ m tall and arising from a limited prostrate portion. Cells were cylindrical or swollen, 7.5–10 μ m wide (Fig. 3B); small pectic caps occurred at the top of many apical cells. Gametangia were abundant, globular in shape, and 15–20 μ m in diameter. In individuals from the Great Highway, the width of the cells was higher (12–16 μ m) and the cell walls were moderately corrugated; based on these characteristics, these specimens were identified as *T. abietina* var. *corrugata*.

After examination of our samples, we conclude that *T. flava* is the dominant species of *Trentepohlia* at coastal sites in the San Francisco region. *Trentepohlia abietina* is also present but, based on our limited sampling, does not appear to be as abundant as *T. flava*. Our results also suggest a possible ecological differentiation between the two species, with *T. flava* able to grow on a wide range of living and nonliving substrates, but *T. abietina* possibly limited to tree bark.

DISCUSSION

Trentepohlia flava is a well-defined species, whose taxonomic circumscription is now well established from the morphological point of view. It was originally described as *Mycinema? flava* by Hooker

TABLE 1. *TRENTEPOHIA* SAMPLING IN CALIFORNIA.

Sample ID	Date	Site name	Location	Latitude	Longitude	Substrate	Species ID
17-1	22-Apr-17	Fort Funston	San Francisco	37.7202	-122.5043	cypress tree along trail on sandy flat adjacent to Pacific Ocean	<i>T. flava</i>
17-2	22-Apr-17	Fort Funston	San Francisco	37.7213	-122.5037	cypress tree along trail on sandy flat adjacent to Pacific Ocean	<i>T. flava</i>
17-3	22-Apr-17	Great Highway	San Francisco	37.7615	-122.5098	cypress tree along highway where urban development meets Pacific Ocean	<i>T. abietina</i> var. <i>corrugata</i> & <i>T. flava</i>
17-4	22-Apr-17	Lands End	San Francisco	37.7841	-122.5086	cypress tree along trail along rocky outcrop ~125 m from Pacific Ocean	<i>T. flava</i>
17-5	22-Apr-17	Lands End	San Francisco	37.7845	-122.5088	cypress tree along trail along rocky outcrop ~150 m from Pacific Ocean	<i>T. flava</i>
17-6	14-Apr-17	Point Lobos	Carmel	36.5215	-121.9512	cypress tree along trail along rocky outcrop adjacent to Pacific Ocean	<i>T. flava</i>
17-7	14-Apr-17	Point Lobos	Carmel	36.5221	-121.9512	cypress branch	<i>T. flava</i>
17-8	14-Apr-17	Point Lobos	Carmel	36.5221	-121.9536	cypress branch	<i>T. flava</i>
17-9	14-Apr-17	Point Lobos	Carmel	36.5227	-121.9520	cypress base branches	<i>T. flava</i>
17-10	14-Apr-17	Point Lobos	Carmel	36.5221	-121.9532	cypress trunk	<i>T. flava</i>
17-11	14-Apr-17	Point Lobos	Carmel	36.5228	-121.9522	dead cypress trunk	<i>T. flava</i>
17-12	14-Apr-17	Point Lobos	Carmel	36.5221	-121.9536	cypress branch exposed to ocean	<i>T. flava</i>
17-13	14-Apr-17	Point Lobos	Carmel	36.5220	-121.9533	dead cypress branch	<i>T. flava</i>
17-14	14-Apr-17	Point Lobos	Carmel	36.5224	-121.9523	cypress branches	<i>T. flava</i>
17-15	14-Apr-17	Point Lobos	Carmel	36.5219	-121.9533	dead cypress branches	<i>T. flava</i>
17-16	14-Apr-17	Point Lobos	Carmel	36.5219	-121.9533	cypress branches	<i>T. flava</i>
17-17	14-Apr-17	Point Lobos	Carmel	36.5219	-121.9537	seaward facing rock	<i>T. flava</i>
17-18	14-Apr-17	Point Lobos	Carmel	36.5222	-121.9530	dead exposed roots	<i>T. flava</i>
17-19	14-Apr-17	Point Lobos	Carmel	36.5220	-121.9533	rock	<i>T. flava</i>
17-20	14-Apr-17	Point Lobos	Carmel	36.5219	-121.9534	cypress branch	<i>T. flava</i>
17-21	14-Apr-17	Point Lobos	Carmel	36.5220	-121.9533	rock	<i>T. flava</i>
17-22	14-Apr-17	Point Lobos	Carmel	36.5222	-121.9537	rock	<i>T. flava</i>
17-23	14-Apr-17	Point Lobos	Carmel	36.5221	-121.9532	cypress tree trunk	<i>T. flava</i>
17-24	14-Apr-17	Point Lobos	Carmel	36.5226	-121.9518	cypress branch	<i>T. flava</i>
17-25	14-Apr-17	Point Lobos	Carmel	35.5221	-121.9527	cypress branch	<i>T. flava</i>
17-26	14-Apr-17	Point Lobos	Carmel	35.5219	-121.9533	cypress branch	<i>T. flava</i>
17-27	22-Apr-17	Presidio 1	San Francisco	37.7874	-122.4704	tree near lake in urban park ~1400 m from Pacific Ocean	<i>T. abietina</i>
17-28	22-Apr-17	Presidio 2 (1st Dr. E) (Lake & 12th)	San Francisco	37.7995	-122.4631	tree in urban development adjacent to cemetery ~600 m from SF Bay	<i>T. abietina</i>
17-29	22-Apr-17	Presidio 3 (Moraga Ave)	San Francisco	37.7976	-122.4583	tree in urban development ~800 m from SF Bay	<i>T. abietina</i>
17-30	2-May-17	Sharp Point	Pacifica	37.6205	-122.4964	cypress tree along trail along rocky outcrop adjacent to Pacific Ocean	<i>T. flava</i>
17-31	22-Apr-17	Sutro Heights	San Francisco	37.7775	-122.5122	cypress tree along trail along rocky outcrop in urban area adjacent to Pacific Ocean	<i>T. flava</i>

TABLE 1. CONTINUED

Sample ID	Date	Site name	Location	Latitude	Longitude	Substrate	Species ID
17-32	22-Apr-17	Sutro Heights	San Francisco	37.7776	-122.5122	cypress branch	<i>T. flava</i>
17-33	22-Apr-17	Sutro Heights	San Francisco	37.7776	-122.5122	cypress branch	<i>T. flava</i>
17-34	22-Apr-17	Sutro Heights	San Francisco	37.7776	-122.5123	wooden fence (unknown wood type)	<i>T. flava</i>
17-35	22-Apr-17	Sutro Heights	San Francisco	37.7777	-122.5124	cypress branch	<i>T. flava</i>
17-36	22-Apr-17	Sutro Heights	San Francisco	37.7775	-122.5122	cypress trunk/large branch	<i>T. flava</i>
17-37	22-Apr-17	Sutro Heights	San Francisco	37.7777	-122.5124	branch	<i>T. flava</i>
17-38	22-Apr-17	Sutro Heights	San Francisco	37.7777	-122.5124	branch	<i>T. flava</i>
17-39	22-Apr-17	Sutro Heights	San Francisco	37.7777	-122.5114	fallen branch	<i>T. flava</i>

and Arnott (1832) based on material collected in Concepcion, Chile, from leaves of *Quadria heterophylla* Ruiz & Pavón (now *Gevuina avellana* Molina). Since Hooker and Arnott (1832) were unsure of the placement at the genus level, *Mycinema? flava* is a taxonomically invalid name and the name of the species was nomenclaturally validated by Kützinger (1843) as *Chroolepus flavum*, the basionym of *T. flava* (Kützinger) De Toni. Cribb (1970) provided a detailed morphological circumscription of *T. flava* based on examination of the type specimen of *Mycinema? flava* and other important herbarium specimens.

Rindi et al. (2009) sequenced the *rbcL* gene in specimens identified by them as *T. flava*, collected from a coastal area of the Atacama Desert, Chile, and from Inverness, Tomales Bay, California (a site located about 200 km up the coast from Point Lobos). Despite the great distance between Chile and California, these specimens had almost identical *rbcL* sequences, strongly supporting the conspecificity of the two populations. This suggests that *T. flava* is a widespread species that has a continuous distribution along the Pacific shores of the Americas. Our specimens from Point Lobos are morphologically identical to both the Chilean and Californian samples sequenced by Rindi et al. (2009) and agree well with the morphological circumscription given by Cribb (1970). Thus, our identification of *Trentepohlia flava* from Point Lobos is strongly supported by morphological evidence (which indirectly suggests also a likely molecular identity of *rbcL* sequence with the material from Inverness and Atacama). The thick, heavily corrugated cell walls and the tall erect axes (unbranched to sparsely branched) make *T. flava* a morphologically distinct alga; these features are very consistent in this species and were also observed in specimens from the Oregon coast (Rindi unpublished data) and southern Africa (Rindi et al. 2006).

Trentepohlia aurea, a name often applied to the Point Lobos algae, is the type species of the genus and was originally described by Linnaeus (1753) as *Byssus aurea* based on collections from Europe (Wales and Italy). The morphological circumscription of this species has been the subject of some debate and numerous subspecific taxa have been erected for it (see Guiry and Guiry 2017). For some time, the distinction of *T. aurea* and *T. flava* was questioned by some authors (Hariot 1889; Printz 1939) who did not separate these entities at the species level; they considered *T. flava* a variety of *T. aurea*, reporting it under the heterotypic synonym *T. aurea* var. *polycarpa* (based on *Trentepohlia polycarpa* Nees & Montagne, now considered a heterotypic synonym of *T. flava*). Cribb (1970), after examination of the type of *Mycinema? flava* and other herbarium specimens, concluded that the two entities are different species, arguing that the wall ornamentation of *T. flava* is a stable character distinguishing it from *T. aurea*. Based on our experience, we agree with Cribb (1970); in the past, one of us (F. Rindi) has examined numerous

specimens of *T. aurea* from Europe, all of which differed substantially from *T. flava* and never showed heavily corrugated walls. Some of these specimens were sequenced in molecular phylogenetic studies (López-Bautista et al. 2006; Rindi et al. 2009) and molecular data supported the species level separation of *T. aurea* and *T. flava*. In molecular phylogenies including samples of both species (Rindi et al. 2009; Nelsen et al. 2011), *T. aurea* forms a strongly supported clade well separated from *T. flava*. During our survey we could not find any specimens morphologically referable to *T. aurea* and we conclude that, at present, the occurrence of this species in the San Francisco region cannot be confirmed.

We refer to *Trentepohlia abietina* the three samples collected at Presidio (1, 2, 3) and to its variety *corrugata*, the sample from Great Highway. *Trentepohlia abietina* was originally described by Kützinger (1845) using material collected from the bark of fir trees (*Abies alba* Miller) at Hirschberg (probably Hirschberg im Riesengebirge, currently Jelenia Góra, southern Poland). The morphological circumscription of this species is generally straightforward and records of it are available for temperate and tropical regions throughout the world (Printz 1939; Sarma 1986; Rindi and Guiry 2002; Rindi et al. 2006). It should be noted, however, that reliable molecular data for this species are scant and currently insufficient for an accurate phylogenetic assessment. López-Bautista et al. (2006) sequenced the small subunit ribosomal RNA region in samples of *T. abietina* from Ireland, which indicated a close relationship with *T. umbrina* (Kützinger) Bornet, *T. jolithus* (Linnaeus) Wallroth, and *Phycopeltis arundinacea* (Montagne) De Toni. However, in subsequent studies other samples morphologically similar to *T. abietina* were recovered in different positions in molecular phylogenies (*rbcL* phylogenies reported by Rindi et al. [2009] and Nelsen et al. [2011]). This suggests the possibility that the morphology of *T. abietina* may be shared by several cryptic species not closely related from a phylogenetic point of view. This would pose a major problem for the correct identification of the species and the correct application of the name *T. abietina*. This issue can be resolved only with a large-scale reassessment of the species, based on a molecular dataset including sequences of specimens from the type locality, Hirschberg, and many other locations covering the whole geographical range of the species. Since such data are currently not available, we base the identification of our specimens on the traditional morphological circumscription of the species established by previous authors (De Toni 1889; Hariot 1889; Printz 1939).

In conclusion, we confirm that specimens from coastal areas of California previously reported as *T. aurea* var. *polycarpa* were correctly identified. However, this alga is no longer considered a variety of *T. aurea* and we recommend that these specimens

should be referred to as *T. flava*, which is presently the accepted name for this alga.

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LITERATURE CITED

- BROOKS, F., F. RINDI, Y. SUTO, S. OHTANI, AND M. GREEN. 2015. The Trentepohliales (Ulvophyceae, Chlorophyta): an unusual algal order and its novel plant pathogen—*Cephaleuros*. *Plant Disease* 99:740–753.
- CHAPMAN, R. L. 1984. An assessment of the current state of our knowledge of the Trentepohliaceae. Pp. 233–250 in D.E.G. Irvine and D.M. John (eds.), *Systematics of the Green Algae*. Academic Press, London.
- AND M. C. HENK. 1986. Phragmoplasts in cytokinesis of *Cephaleuros parasiticus* (Chlorophyta) vegetative cells. *Journal of Phycology* 22:83–88.
- CRIBB, A. B. 1970. A revision of some species of *Trentepohlia* especially from Queensland. *Proceedings of the Royal Society of Queensland* 82:17–34.
- DE TONI, G. B. 1889. *Sylloge algarum omnium hucusque cognitarum*. Vol. I. Chlorophyceae. Patavii [Padua]: Sumptibus auctoris.
- GUIRY, M. D. AND G. M. GUIRY. 2017. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org> [accessed 25 May 2017].
- HARIOT, P. 1889. Notes sur le genre *Trentepohlia* Martius (Suite). *Journal de Botanique (Morot)* 3:393–405.
- HOOKE, W. J. AND G. A. W. ARNOTT. 1832. *The botany of Captain Beechey's voyage; comprising an account of the plants collected by Messrs Lay and Collie, and other officers of the expedition, during the voyage to the Pacific and Bering's Strait, performed in His Majesty's Ship Blossom, under the command of Captain F.W. Beechey, R.N., F.R. A.S. Henry G. Bohn, London.*
- KÜTZING, F. T. 1843. *Phycologia generalis oder Anatomie, Physiologie und Systemkunde der Tange*. F.A. Brockhaus, Leipzig.
- . 1845. *Phycologia Germanica*. Wilhelm Köhne, Nordhausen.
- LINNAEUS, C. 1753. *Species plantarum*. Vol. II. Impensis Laurentii Salvii, Stockholm.
- LÓPEZ-BAUTISTA, J. M. AND R. L. CHAPMAN. 2003. Phylogenetic affinities of the Trentepohliales inferred from small-subunit rDNA. *International Journal of Systematic and Evolutionary Microbiology* 53:2099–2106.
- , F. RINDI, AND M. D. GUIRY. 2006. Molecular systematics of the subaerial green algal order Trentepohliales: an assessment based on morphological and molecular data. *International Journal of Systematic and Evolutionary Microbiology* 56:1709–1715.
- , D. A. WATERS, AND R. L. CHAPMAN. 2002. The Trentepohliales revisited. *Constancea* 83.1.
- NELSEN, M. P., E. RIVAS PLATA, C. J. ANDREW, R. LÜCKING, AND H. T. LUMBSCH. 2011. Phylogenetic diversity of trentepohlialean algae associated with lichen-forming fungi. *Journal of Phycology* 47:282–290.

- PRINTZ, H. 1939. Vorarbeiten zu einer Monographie der Trentepohliaceen. *Nytt Magasin for Naturvidenskapene* 80:137–210.
- RINDI, F. AND M. D. GUIRY. 2002. Diversity, life history, and ecology of *Trentepohlia* and *Printzina* (Trentepohliales, Chlorophyta) in urban habitats in Western Ireland. *Journal of Phycology* 38:39–54.
- , ———, AND J. M. LÓPEZ-BAUTISTA. 2006. New records of Trentepohliales (Ulvophyceae, Chlorophyta) from Africa. *Nova Hedwigia* 83:431–449.
- , D. W. LAM, AND J. M. LÓPEZ-BAUTISTA. 2009. Phylogenetic relationships and species circumscription in *Trentepohlia* and *Printzina* (Trentepohliales, Chlorophyta). *Molecular Phylogenetics and Evolution* 52:329–339.
- SARMA, P. 1986. The freshwater Chaetophorales of New Zealand. *Nova Hedwigia Beiheft* 58:1–169.
- WIGGERS, F. H. 1780. *Primitiae florae holsaticae*. Litteris Mich. Frider. Bartschii Acad., Kiel.